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THE ADAPTABILITY OF METABOLISM IN NORTH CASPIAN MUSSELS (GENUS DREISSENA[1]) TO VARIATION IN SALINITY REGIME [Prisposoblennost' obmena dreissen severnogo kaspiya k izmeneniyu solevogo rezhima]

By

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The problem of the development of saltwater fauna and its adaptation to the surrounding medium is being studied by many scientists. Specific problems connected with the effects of the salinity of the medium on the organism or on its physiological processes were studied by Schmankewitsch [13], Gayevskaya [4], Beklemishev [3], Tarusov, [8], Schlieper [14, 15, 16], Beadle [9], Schwabe [17], and many others. The water and salinity problem as a whole was mainly studied by L.A. Zenkevich [5] and his school and abroad by Remane [12] and others.

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[1] [Translator's note: Term used by author.]

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A study of the conditions in which organisms can survive in salt waters is very important for us, since many of our seas (the Baltic, Caspian, Azovsk, Aral Seas) are completely salinated and other seas (Black, Karsk, Laptev Sea, etc.) are partially salinated. Usually these seas and regions are used extensively for different purposes in the economy.

In the study of the adaptation of organisms to salt waters, their salinity interaction with the medium is of first-order importance. Very often due to the instability of the salinity regime, many inhabitants find themselves in unfavorable conditions, which has a harmful effect on their metabolism, growth, reproduction, etc. Some forms wither or even vanish altogether and other forms develop on a large scale. Instability in the composition and number of saltwater inhabitants may have an effect on the industrial productivity of the water basin.

We considered it necessary to study in greater detail the effect of a change in the salinity of the medium on various physiological processes in the main forms inhabiting the Caspian Sea. The following processes were studied: respiration, osmoregulation, the formation of concha, growth, reproduction and propagation through the habitat of molluscs, from the standpoint of their adaptation to the surrounding conditions.

In this article we only describe the results of experiments dealing with the effect of a change in salinity of the medium on the oxygen requirements of northern Caucasus Dreissena and we attempted to establish the salinity limits within which their energy metabolism can take place.

A large number of studies dealing with the connection between the rate of the metabolism and the salinity of the medium is available in the literature [2, 6, 8, 16, 17]. These studies touch on various aspects of the

respiratory process of certain marine organisms, and they provide much valuable material which enhances our understanding of the phenomenon. However, all problems are far from solved and our data can shed additional light on some problems.

I am deeply grateful to Prof. L.A. Zenkevich and Prof. A.A. Shorygin for their valuable advice and help in this study.

Material and Method

Dreissena polymorpha inhabits the Volga region and the entire Caspian region, in a large number of subspecies. Another form of Dreissena, described by Brusinova as a special species, the Dreissena andrusovi also inhabits the the northern Caucasus. The latter species resembles both Dr. polymorpha and Dr. caspia. According to Andrusov, it also has many varieties like Dr. polymorpha.

By the shape of the concha, the Dreissena from the Volga region is closest to Dr. polymorpha v. fluviatilis described in Andrusov's study [1]. The Dreissena from the Chapur'ye spit undoubtedly has the greatest affinity with Dr. polymorpha v. iluviatilis, but the walls of its concha are thinner. The Dreissena from the eastern half of the northern Caspian (Zaburun'ye, Gur'yevskaya furrows) differ from the western Dreissena (Volga-Chapur'ye spit); the former resembles the new species Dr. andrusovi described by Brusina, and the latter the Dr. caspia. The western Dreissena is larger than the eastern Dreissena, in the former the predominant size is 13-17 mm to 32 mm, and in the latter, 6-10 mm to 16 mm when both Dreissena are juvenile.

Before the experiments, all organisms were kept in the same water which they inhabited in the sea or river.

Waters of different salinities were obtained from seawater by evaporation in the sun or by dilution with fresh water (Zenkevich [5], Karpevich). The salinity of the water was determined from the chlorine.

The molluscs were washed, counted, dried on filter paper and weighed before the experiment.

The oxygen consumed by the organisms was determined in closed containers using the Winkler method at a 18-19°C temperature and the duration of the experiment was 5-6 h. The experiment usually ended before 40-50% oxygen was consumed in the optimal salt media in the containers. In the control containers, the oxygen content varied in this time by no more than 0.01 cm^3 per liter and it was not taken into account in the subsequent calculations.

Since our task was to determine the stability of the optimal zones and the lethal salinity points for the metabolism of the Dreissena, we developed the method of "physiological adaptations," i.e. we used two methods in the experiments: in some cases, the organisms were immediately transplanted into respiratory containers to which water with a 0.2, 5.7, 9, 11, 13, 15 and 17 °/oo salinity was added (abrupt change) and after the experiment they again were returned to their usual medium. In other cases, the organisms were gradually conditioned to inhabit different media. In this series of experiments, the salinity in the crystallizing vessel was changed every 2 days by 2 °/oo ("gradual change").

The rate of change of the salinity of the medium adopted by us (2 °/oo every 2 days) can be considered to be correct, since in this period the internal and external medium was equalized among the molluscs not only as a result of the water but also the salt metabolism.

When each group of organisms attained the salinity prescribed for it, the respiration was determined simultaneously in all groups in order to avoid differences in temperature, illumination, etc.

Results of Experiments

A. Oxygen Use During an Abrupt Change in the Salinity of the Medium

The material used in the experiments consisted of individuals of different sizes. Therefore we first tried to clarify how organisms of different ages react to a change in the salinity of the medium. With this purpose in mind we determined among the Dreissena from the Volga River delta their age and divided them into three groups: 1) length 25-30 mm, 12-15 years; 2) length 15-17 mm, 5-6 years; 3) length 7-13 mm, 1.5-3 years (young). Two-three series of experiments with an abrupt change in the salinity regime were made with each group (see table).

As we expected, young Dreissena require relatively larger amounts of oxygen (per 1 g/h) than adult Dreissena. But all Dreissena react in the same way to a change in the salinity regime. The organisms from the Volga delta use up the largest amount of oxygen in water with salinity 0 to 2%, i.e. in their natural salinity and in salinity close to it. At 5 °/oo, the amount of oxygen used decreases, and at 7 °/oo apparently respiration ceases altogether. The immersion of the molluscs in this salinity has a highly unfavorable effect on their metabolism, however they do not die for 5-6 h, they only obdurate their conchi and quickly recover when replanted in fresh water. When left in water with 7 °/oo salinity for a comparatively long time, all of them died gradually.

The average length of the Dreissena from the Chapur'ye spit was about 15-17 mm and their age varied from 3 to 6 years. Because of their very thin-walled

Effect of salinity of the medium on the oxygen used up by Dreissena from various North Caspian regions

Район обитания животных (a)	Средний вес одного экземпляра, г (b)	Температура, при которой проводились опыты (c)	Соленость среды обитания (‰) (d)	e Потребление кислорода в см³ на 1 г в 1 час при солености в ‰ 0	2	5	7	9	13	15	17	19	Колич. серий (f)	Колич. опытов (g)
h Резкая смена солености среды														
i Дельта р. Волги	1,8—1,52	18—20	0	0,0156	0,0198	0,0152	0,0075	0,0069	0,007	—	—	—	4	24
» » »	0,8	15—17	0	0,022	0,022	0,012	0,0045	0,006	—	—	—	—	2	10
» » »	0,08	18—19	0	0,038	—	0,02	0,007	0,009	—	—	—	—	2	8
j Чапурья коса	0,3	18	0—2	0,148	0,0165	0,015	0,0137	0,005	0,004	—	—	—	2	12
k Забурунье, ст. 9	0,06	18	4—7	0,024	0,023	0,04	0,053	—	0,038	0,029	0,026	0,016	3	24
l Восточный участок, ст. 32	0,07	18—19	10,9*	0,017	0,035	0,055	0,034	—	0,043	0,030	0,024	0,022	3	24
													16	102
m Постепенная смена солености среды														
i Дельта р. Волги	0,6	11—15	0	0,014	0,014	0,016	0,015	0,013	0,014	0,018	n Погибли		1	7
» » »	0,7	15—18	0	0,023	0,023	0,021	0,0195	0,027	0,02	0,018	0,021	0,018	3	27
j Чапурья Коса	0,3	18—19	0—2	0,0165	—	0,017	0,015	0,015	—	0,013	0,02	—	1	5
k Забурунье, ст. 9	0,03	19	5—7	0,025	0,027	0,027	0,035	0,03	—	0,022	0,03	—	2	14
» ст. 12	0,04	20—24	4,5—5	0,035	0,038	0,033	0,035	0,036	0,045	0,038	0,032	0,027	3	27
» ст. 12	0,04	24—29	4,5—5	0,056	0,058	0,048	0,053	0,055	0,054	0,040	0,030	0,037	3	27
													13	107

*Dreissena detected at this salinity

Key:
a. Habitat region of organisms
b. Average weight of one individual
c. Temperature at which experiments were carried out
d. Salinity of habitat medium
e. Oxygen use, cm^3/g per h, with salinity ($^o/oo$)
f. Number of experiment series
g. Number of experiments
h. Abrupt change in salinity of medium
i. Volga River delta
j. Chapur'ye spit
k. Zaburun'ye, Station 9
l. Eastern Sector, station 32
m. Gradual change in salinity of medium
n. Died

[Note: Commas in numerals are equivalent to decimal points.]

concha, the required oxygen indices for them were somewhat lower than for the Volga Dreissena. In natural conditions, the Dreissena from the Chapur'ye spit are usually subjected to small fluctuations in the salt concentrations and are therefore less sensitive to an abrupt change in the salinity of the medium than inhabitants of fresh water.

The amount of oxygen used up by the Dreissena from the Chapur'ye spit remains constant in media from 0 to 5 °/oo and nearly normal, at 7 °/oo the intensity of the metabolism is somewhat reduced and at 9 °/oo it ceases altogether. Both Dreissena use up similar amounts of oxygen. These Dreissena belong to similar related groups and the difference that was detected undoubtedly depends on the conditions in the habitat.

The Dreissena from the eastern salinity sectors of the northern Caspian are smaller. The mean length of their concha is 10-12 mm and their age is 4-5 years. These forms live in treacherous salinity regime conditions, since certain sectors before the Ural River delta were desalinated in 1941 in the period between the spring and summer by 3-5 °/oo. The Dreissena form very large clusters here.

The curves for the use of oxygen by the eastern Dreissena during an abrupt change in the salinity of the medium differ basically from the curves obtained in the preceding experiments. These are unimodal curves with the maximum indices in the interval 5 to 10-11 °/oo. Thus also here the optimum respiratory conditions lie in the salinity range of natural habitat waters.

The size of the beneficial salinity range (5-10 °/oo) for these forms does not seem to depend on the salinity of the medium inhabited by the organism. The curves for the use of oxygen for organisms inhabiting water with 4 °/oo and 10 °/oo salinity coincide.

In unfavorable conditions, the eastern Dreissena do not close their conchae and do not isolate themselves from the environmental conditions. Respiration is possible for a short time even in media with 19 and 20 °/oo salinity. Apparently these Dreissena react less actively to a change in the salinity; however, they cannot survive in the limiting media.[1]

Thus the experiments made by us enabled us to determine the beneficial salinity boundaries for the respiration of the Dreissena. For the western and eastern Dreissena, the beneficial salinity boundaries are different and clearly marked. Salinity fluctuations in these intervals undoubtedly had no harmful effect on the main physiological processes. However, the experiments did not enable us to determine the actual resistance of the Dreissena to a change in the salinity regime in the entire salinity interval.

B. Amount of Oxygen Used During Gradual Change of Salinity Regime

In this series of experiments the salinity of the natural habitat medium of the organisms was gradually changed toward desalination or salination. In the preliminary experiments it became clear that all Dreissena can survive for a certain time in media with salinity from 0 to 17-19 °/oo. Therefore, their adaptation period was 12 to 14 days when the initial salinity was 4-5 °/oo and 16-18 days in fresh water forms. The adaptability of the Dreissena or the physiological adaptation of the organism to higher salinities was unstable and exceptionally brief. Thus, in media with salinity above 11 °/oo, the number of deaths among the organisms increased, and for the limiting salinity (17 °/oo), it was as large as 50% per day. When transplanted from 17 to 19 °/oo salinity, almost all organisms died.

[1] Data on the survival of Dreissena were published in DAN, 1947.

within 1 day. The death was caused by an abrupt disturbance in the osmoregulatory processes.

The table gives the mean amounts for the oxygen use which were obtained on the basis of data from several series of experiments separately for each group of Dreissena. All Dreissena had one phenomenon in common, namely notwithstanding the fact that at salinities above 10 °/oo causing progressively increasing deaths, the living individuals used the same amount of oxygen as in their natural habitat medium. For example, the Volga Dreissena, a typical freshwater form, when gradually transplanted from fresh water into waters with different salinities did not close its concha at 7-9 °/oo as in the experiments with the abrupt change in the saltwater concentrations, but it retained at 13-15 °/oo a metabolism whose rate was almost the same as in fresh water, i.e. its salinity metabolism range was increased to 8-10 °/oo.

Dreissena from the Chapur'ye spit also survived for a certain time in media with salinity from 0 to 15-17 °/oo, retaining normal respiration. Such unusual tolerance to increased salinity concentrations among freshwater groups led us to assume that among the eastern forms the salinity range will be further increased. However, this did not occur.

The preparations for the experiments were made in the same way as in the preceding series. We were not able to maintain a standard temperature in all series -- three series of experiments were carried out at a 20-25°C temperature, three series at a 24-29°C temperature, and only one series at an 18°C temperature. Both the eastern and western Dreissena retained at 18°C the same respiratory intensity in all salinity media (from 0 to 17 °/oo) regardless of the fact that salinities above 10 °/oo increased their death rate.

In water with 19 °/oo salinity, they died quickly, since they were not able to adapt to this concentration. At 20-24°C temperatures, the amount of oxygen used was more or less close to the optimum amount only in media with salinity from 0 to 15 °/oo and it dropped at 17 °/oo. This forced us to carry out experiments also at the extreme 24-29°C temperatures. It turned out that at such temperatures, nearly optimal breathing was retained only in media with salinity from 0 to 11 °/oo, and that the oxygen used dropped considerably at 13, 15 and 17 °/oo salinity. Apparently the unfavorable effect of higher salt concentrations is aggravated at higher temperatures.

Comparing the curves for the oxygen use during an abrupt and gradual change in the salinity among the eastern Dreissena, we established that during their physiological adaptation their salinity range is not increased towards higher salt concentrations and that it increases only by 2-3 °/oo in the direction of fresh water.

Saltwater Dreissena survived 19-20 °/oo salinities a little longer than freshwater Dreissena, but the number of survivors was very small and they reacted so feebly to stimuli that it was not possible to carry out respiration experiments.

When the same curves are compared, one can clearly see the difference in the rate of the metabolism in the optimal zone among the eastern Dreissena during an abrupt change in the salinity regime, and among the gradually adapting Dreissena in the same zone (4-9 °/oo). In the first case the rate is high (0.04-0.05 cm^3 per 1 g weight per 1 h) and in the second case it is lower (0.027-0.034). This can be explained by the fact that the experiments with the abrupt change in the salinity regime were carried out in July, a period of intense reproduction of these forms, and

the experiments with the gradual change were carried out in September, a time when the reproduction period came nearly to an end. It is possible that the difference in the biological state had an effect on the rate of the metabolism.

Evaluation of Results

Summarizing the data that were obtained, it should be mentioned that the method used for studying the character of the metabolism of the Dreissena during abrupt and gradual salinity changes in the medium yielded favorable results. The usually used method (abrupt change in the salinity) in the study of the effect of the medium on the organism will undoubtedly make it possible to determine the optimum zone in which the fluctuations in the salinity factor do not have a harmful effect on the physiological processes (natural adaptation zone).

The effect of gradual changes in salinity will make it possible to determine the entire salinity range in which the physiological processes can take place among individuals of a given species. This metabolism range is much larger than the interval in which the Dreissena can actually survive.

In the first case (abrupt change) we obtain a clear characteristic adaptation of the metabolism to fluctuations in the salinity in the natural habitat zones and detect the ability of the organism to quickly adjust its metabolism to catastrophic disturbances in the salinity conditions, whereas in the latter case (gradual change), we detect the ability of the organism to survive unfavorable conditions and the adaptation characteristics of the organism.

The tolerance to slow salinity changes is very high among the Dreissena and equal for all groups[1] in spite of a number of differences. None of the groups of Dreissena which were studied can survive in the entire interval, they have only the capacity to temporarily survive in unusual conditions. Therefore, we called this property the "potential metabolism resistance" for the given form.

However, the potential resistance of all Dreissena is not accidental, it indicates the close affinity of the groups that were studied and also apparently the salinity limit for the given species or genus. The latter is possible when we recognize that the western freshwater Dreissena, Dr. polymorpha, and the eastern, saltwater Dreissena, Dr. andrusovi, are already established species. Since these forms have their own habitats, the simplest assumption is that we are dealing with subspecies of the same species.

Our experiments have shown that the Dreissena are not as euryhaline as would seem at first glance, and that local groups with specific physiological and morphological characteristics exist.

Conclusions

1. In Dr. polymorpha v. fluviatilis from the Volga region, a 5 °/oo increase in salinity resulted in a marked drop in the intensity of respiration. A 7 °/oo salinity increase causes a complete cessation of the respiration. In Dr. polymorpha from the Chapur'ye spit, respiration ceased during an 8-9 °/oo increase in salinity.

2. In eastern Dreissena, Dr. andrusovi, a 5 °/oo increase in the salinity does not have a noticeable effect on the respiratory intensity.

[1] Dr. polymorpha from the Chapayevka River and the Aral Sea reacted in the same manner.

A 10 °/oo increase causes a considerable decrease in the respiratory intensity. Abrupt desalination also depresses the respiration.

3. The salinity interval in which metabolism is possible among Dreissena during an abrupt change in the salinity of the medium for each form is well defined, for the Volga Dreissena from 0 to 6 °/oo, for the Chapur'ya Dreissena from 0 to 9 °/oo, and for the eastern Dreissena from 0 to 19 °/oo. The maximum oxygen use was observed in media which were close to natural media, i.e. from 0 to 2 °/oo, from 0 to 5 °/oo, and from 5 to 10 °/oo for each group, respectively.

4. When the salinity was gradually changed, the respiration was retained in all groups in the interval from 0 to 17 °/oo (temperature 18-20°C). However, in salinities above 10 °/oo, the organisms gradually die (the cause of their death is the disturbance of the osmoregulatory processes).

5. The method of physiological adaptations that was applied made it possible, on the one hand, to determine the optimal and lethal salinity metabolism zones for each ecological group of organisms living in confined natural salinity conditions, and, on the other hand, made it possible to determine their "potential resistance."

6. The potential metabolism resistance for all Dreissena that were studied turned out to be the same. This indicates the close affinity of various groups of Dreissena. Hence, the potential resistance is a characteristic feature of the species or even the genus.

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